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Vision Research 45 (2005) 2231–2243

Vision Research

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A binocular rivalry study of motion perception in the human brain

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Received 17 September 2004; received in revised form 7 February 2005

Abstract

The relationship between brain activity and conscious visual experience is central to our understanding of the neural mechanisms underlying perception. Binocular rivalry, where monocular stimuli compete for perceptual dominance, has been previously used to dissociate the constant stimulus from the varying percept. We report here fMRI results from humans experiencing binocular rivalry under a dichoptic stimulation paradigm that consisted of two drifting random dot patterns with different motion coherence. Each pattern had also a different color, which both enhanced rivalry and was used for reporting which of the two patterns was visible at each time. As the perception of the subjects alternated between coherent motion and motion noise, we examined the effect that these alternations had on the strength of the MR signal throughout the brain. Our results demonstrate that motion perception is able to modulate the activity of several of the visual areas which are known to be involved in motion processing. More specifically, in addition to area V5 which showed the strongest modulation, a higher activity during the perception of motion than during the perception of noise was also clearly observed in areas V3A and LOC, and less so in area V3. In previous studies, these areas had been selectively activated by motion stimuli but whether their activity reflects motion perception or not remained unclear; here we show that they are involved in motion perception as well. The present findings therefore suggest a lack of a clear distinction between 'processing' versus 'perceptual' areas in the brain, but rather that the areas involved in the processing of a specific visual attribute are also part of the neuronal network that is collectively responsible for its perceptual representation.

Keywords: Motion perception; Binocular rivalry; Functional imaging; Consciousness

1. Introduction

The relationship between brain activity and perception is of central interest in systems neuroscience (e.g. Crick & Koch, 1992). Studies seeking to understand this relationship face the problem of dissociating the perceptual from the sensory representation of a stimulus. A visual stimulus, for example, will typically elicit responses in many different visual structures, even in an anesthetized subject. To concentrate on neural activity that is directly related to perceptual processing, often perceptual illusions or puzzle figures are employed, the perception of which changes over time without concomitant change in the stimulus itself. Binocular rivalry (BR) is one celebrated example; it refers to the stochastic changes of perception during dichoptic visual stimulation (Blake, 1989; Levelt, 1965). By monitoring brain activity under such conditions of constant stimulus and alternating perception, one might hope to distinguish between areas responding to the former and those with a response that is dictated by the latter. This idea has been previously applied in monkey electrophysiology experiments (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997) and revealed the existence of perceptually modulated neurons throughout the visual brain. The low percentage of these neurons in early areas has been recently challenged by human fMRI studies, showing that BR

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0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.02.007

can modulate brain activity as early as V1 (Polonsky, Blake, Braun, & Heeger, 2000), even at monocularly-driven regions of this area (Tong & Engel, 2001). Therefore, unless the reported early effects are solely due to a feedback from later areas, it is unlikely that BR is resolved exclusively at some higher level of the visual pathway. On the other hand, the existence of higher-area neurons which are not modulated by binocular rivalry alternations, excludes the possibility that BR is once and for all resolved in V1. Finding the site at which rivalry is resolved is not an easy task, especially using fMRI where an effect due to the modulation of a subpopulation of neurons in an area does not necessarily generalize over the rest of the area. Furthermore, findings regarding BR of one type of stimulus might not apply to another type. The whole issue is therefore still under investigation, the most recent evidence probably supporting a view of rivalry as a series of processes, each of which is implemented by neural mechanisms at different levels of the visual hierarchy (Blake & Logothetis, 2002).

In the present study, we have combined BR with fMRI to see which visual motion-processing areas of the human brain modulate their activity with respect to the motion percept. Unlike in the electrophysiological studies mentioned above, an advantage of using fMRI is that we were able to look at several brain areas at the same time, under identical and simultaneous stimulation. In this way, the distribution of perceptual correlation across the system can be directly assessed. Here we have focused on the motion system, one of the most extensively studied functionally-specialised systems in the brain. In the monkey, directionally selective cells can be found as early as V1, mostly located in layers 6 and 4B (Gouras, 1974; Hawken, Parker, & Lund, 1988; Hubel & Livingstone, 1990), and a smaller proportion in area V2, mostly encountered in the thick cytocrome oxidase stripes of this area, which receive their input from layer 4B of V1 and in turn project to area V5 (DeYoe & Van Essen, 1985; Livingstone & Hubel, 1987; Shipp & Zeki, 1985; Shipp & Zeki, 1989). The proportion of motion-sensitive cells increases considerable in some of the dorsal higher visual areas. The vast majority of neurons in area V5, for instance, are tuned to the direction of motion of the stimulus (Zeki, 1974), and also to the strength of the motion signal (Newsome, Britten, & Movshon, 1989). In addition to the monkey work, several human fMRI studies have shown that a network of brain regions in the visual cortex is devoted to motion processing (Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; Tootell et al., 1995; Zeki et al., 1991). In other words, there exist a distributed system across the brain, responsible for the processing of visual motion information. However, most electrophysiological studies investigating into the neuronal correlate of motion perception have been concentrating on area V5/MT. Electrically stimulating this area during a motion discrimination task, can alter the perception of the animal towards the direction of motion encoded by the stimulated neurons (Salzman, Britten, & Newsome, 1990), although it is not clear whether microstimulation induces more 'stimulus' or more 'percept'. Under conditions of constant random-dot stimulation, variations in the animal's responses have been found to correlate with the firing of V5 neurons (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996). A similar result has been reported in V5 using binocular rivalry (Logothetis & Schall, 1989), structure-from-motion (Bradley, Chang, & Andersen, 1998) but not apparent motion (Williams, Elfar, Eskandar, Toth, & Assad, 2003). In the human, most studies on motion perception are restricted to V5/MT as well (see Section 4). Here, we used the global nature of fMRI to simultaneously examine how the activation of different brain areas is correlated to alterations in motion perception under constant stimulation conditions. Our results verify the importance of V5 in motion perception and go further to show that, among all visual areas, it has the strongest correlation with motion perception. We also show, however, that V5 is not the only area with activity reflecting the motion percept, but that the latter is rather represented within a network of visual areas previously shown to be involved in motion processing.

2. Method

2.1. Participants

Three male and three female subjects, aged between 20 and 32, were used for this experiment. All had normal or corrected-to-normal visual acuity and normal stereo-depth perception. They all reported vigorous BR (alternating periods of exclusive perceptual dominance) when presented with a different image in each eye, in a prior psychophysical session. In addition to the main experiment, subjects were also scanned using the three localiser stimulation paradigms (retinotopy, V5 and LOC) described below.

2.2. Apparatus and stimuli

Psychophysical stimuli where created on an Apple Macintosh G4 laptop, using the Psychophysical Toolbox software. Stimuli were presented via a back-projection system to a mirror mounted 20 cm above the subject's eyes. A second PC was used to record the responses of the subject, so that the continuous button pressing (see below) would not interfere with the speed of the stimulus presentation. The two computers where synchronized via a TTL pulse send by the scanner at the beginning of each scanning session. For the BR

scans, two different random dot movies (one green and the other red) were superimposed inside a circlular aperture extending 4° in diameter, outlined by a white contour and having a white fixation spot in the center. Both the fixation spot and the surrounding circle were visible to both eyes throughout the scanning session. The two movies were dichopticaly separated using a red filter over one eye and a green filter over the other eye. In cases in which pixels from the two independent movies fell on exactly the same position on the computer screen, they were made yellow so that they would be visible by both eyes. Filter placement over the eyes was counterbalanced across the six subjects. The dot motion coherence of one of the two movies was 0% (all the dots moving randomly) and of the other 50% (half of the dots moving with the same velocity and the other half randomly). The coherently moving dots of the latter case were two-frame rather than continuous, i.e. the direction of motion could not be inferred by following any of the dots, and no specific form-pattern was created from the motion. Perceptually, the 50% and 0% movies appeared homogeneous and identical in terms of form and depth vision, but strongly differed in their motion percept. In this way, we ensured that any differential activation that we get would be purely due to changes in motion information. A coherence level of 50% was used because it was the strongest motion signal that still gave a fairly balanced rivalry with the 0% noise (motion dominance: 6.8 ± 3.1 s, noise dominance: 5.8 ± 2.7 s). The colour of the random dot movie with the coherent motion as well as the eye to which it was presented was constant during a single scanning session but varied across scans. At the beginning of each experiment, the two colours were made roughly equiluminant using the flicker-fusion method. Every subject run an even number of scanning sessions, so that the colour of the motion stimulus was as many times red as it was green. Each scanning session consisted of three 75-s blocks of rivalry presentation, interleaved between four 15-s blocks during which no stimulus but only the fixation cross and surrounding aperture were present on the screen. Subjects were asked to fixate throughout the scanning session, which in total lasted approximately 5 min ($3 \times 75 + 4 \times 15$ s). Under these conditions of dichoptic presentation, BR between the red and the green random dots developed and subjects reported upon their perception using two buttons, one in each hand. Perception of the red dots was indicated by holding down the right-hand button, and perception of the green dots by holding down the left hand button. Piecemeal rivalry, usually present during the transition from one dominance phase to the other, was indicated by releasing both buttons. Cases in which both buttons were depressed together at the same time were also considered as piecemeal rivalry. Four different conditions were thus possible: fixation only, perception of green only, perception of red only, mixed red/green perception. To get an idea of the differences in activation across the different areas caused by 50% versus 0% motion, we also repeated the above experiment in half of the subjects using physical alternations instead of binocular rivalry.

In order to delineate the various visual areas in each subject, we used additional retinotopy and localiser scans. For the V5 localiser scans, low contrast expanding/contracting versus stationary concentric rings were presented to each subject. For the LOC localizer scans we used grayscale images of novel and familiar objects as well as scrambled versions of each set. For the localizer scans of the early retinotopic regions we used rotating, counter-flickering triangular wedge stimuli for the mapping of the borders between visual areas (Sereno et al., 1995). For all localiser scans, the subjects were also instructed to fixate at the center of the display.

2.3. Imaging

For all the experiments scanning was done on the 3T Siemens scanner at the University Clinic in Tübingen, Germany. A Gradient Echo pulse sequence (TR = 2 s, TE = 90 ms for the localizer scans; TR = 1 sec, TE = 40 ms for the event-related scans) was used. Eleven axial slices (5 mm thick with 3.00×3.00 mm in-plane resolution) were collected with a head coil, so as to cover the whole extent of the visual brain. The first eight images of each session were discarded, to allow for T1 equilibration effects. A T1-weighted anatomical image was also acquired, at the end of each experimental session.

2.4. Eye movements

Eye movements were measured in 3/6 subjects, using an EYELINK eye-tracking system, able to give eye position, blink and saccade (based on eye velocity and acceleration signal) information. The frequency, mean amplitude and direction of saccades were extracted in the analysis, together with the distribution of the eye positions with respect to the fixation point.

2.5. Data analysis

fMRI data were processed using the BrainVoyager 4.6 and Matlab 6.0.0.88 (R12) software packages. Preprocessing of all the functional data included head movement correction and removal of linear trends. The 2D functional images were aligned to 3D anatomical data and both were transformed to Tailarach coordinates, in order to compare our area locations to previous studies. The gray-white matter was segmented using the 3D anatomical dataset of each subject and the brain surface was reconstructed and inflated. For each individual subject, the Regions of Interest (ROIs)

defined were visual areas V1, V2, V3, V3a, V4, V5 and LOC. 3D statistical maps were calculated for each one of these ROIs by correlating the signal time course with a reference function for each voxel based on the hemodynamic response properties. Area V5 was defined as the set of voxels in the vicinity of the ascending limb of the inferior temporal sulcus that showed significantly stronger activation (linear correlation, $r = >0.3$, $p < 10^{-3}$) to moving than to stationary rings. Area LOC was defined as the set of continuous voxels in the ventral occipitotemporal cortex that showed significantly stronger activation ($p < 10^{-4}$) to intact than scrambled images based on the average data from the localizer scans. The early visual areas were identified based on standard retinotopic mapping procedures (Sereno et al., 1995).

For the analysis of the BR data, seven volumes (s) after the onset and seven volumes before the offset of stimulation were discarded in order to avoid rapid signal changes related to stimulus/no-stimulus transitions. Also, for a 'green' or 'red' response to be included in the analysis, the perception had to persist for at least 2 s. Most periods of dominance were a couple of seconds long, so this value was a good balance between having enough events to analyse and also give the MR signal change enough time to reliably reflect undergoing neural mechanisms. For each event-related scan, the fMRI response was extracted by averaging the data from all voxels within each of the independently defined ROIs. The averaging was done at each of 15 corresponding time points (s), from −4 to +10 (time 0 being the time of the report). The single-event, averaged-across-voxels activity data was sorted (to the nearest second) relative to the time of each event and converted to percent signal change, with respect to the baseline (mean activity between −6 and −3). The resulting time courses were then averaged between all similar events in all scanning sessions, separately for each individual subject. For group results, similar-event averaging was done across all subjects, with each ROI being defined at the subject-level. In addition to calculating the mean and standard errors of the MR signal with respect to time, we also collapsed time and used a Wilcoxon ranksum test to further quantify differences between the two perceptual conditions, motion and noise. This is a test analogous to the t-test but non-parametric, i.e. makes no prior assumption about the way the data is distributed and is thus more robust. Assuming a normal distribution for our data would be incorrect since, after collapsing time (between −4 and +10), the resulting data was the sum of 15 different normal distributions (one for each time-point). We compared perceive-motion and perceive-noise MR signals and got p values showing how probable it was for the medians of the distributions of the two data sets to be equal. Before looking at p values of individual areas, a two-way analysis of variance was performed to test for a statistically significant interaction between condition (motion, noise) and visual area as factors.

3. Results

In order to investigate the relationship between motion perception and cortical activation in several visual areas, we used localiser stimuli enabling us to identify and separate these areas. Fig. 1 demonstrates the stimuli used for this purpose, as well as the resulting area separation and identification. In the left panel the retinotopic map of a subject is shown on the extracted cortical surface as well as on the inflated left hemisphere. The delineation and marking of the borders between areas V1, V2, V3 and V3a in the dorsal surface presented here was done using the reversals of the retinotopic map on the vertical (orange) and horizontal (yellow) meridian representations between the areas. Similarly, the borders were delineated on the ventral surface of the left hemisphere as well on the dorsal and ventral surfaces of the right hemisphere for all subjects. Stimuli used to localize areas V5 (low-contrast, moving versus stationary rings) and LOC (intact versus scrambled objects) are shown in the right panel together with an example of the resulting activated regions. Since these localiser stimuli were larger than our random dot movies, we also used the statistical contrast between random dot stimulation and fixation to see which part of the cortex was activated by our stimuli. We were thus able to define the different regions of interest (ROIs) for each subject individually, and study the effect of BR stimulation on them.

A schematic representation of the stimuli used in the main study is shown in Fig. 2a. The red dots (shown here to the left eye) all move in random directions and therefore do not produce any coherent motion signal along any particular direction. For the green dots (presented to the right eye), at any point in time, half of the dots were moving upwards giving rise to the perception of upward motion. Under these circumstances, subjects experience vigorous BR between the two conflicting monocular inputs, with alternating periods of green and red dominance separated by shorter periods of a mixed percept. We used the responses of each subject in order to attribute his/her recorded MR signal into conditions of either motion or noise perception, and study any possible differences between the two. As an example, Fig. 2b shows the raw MR signal in area V5 of a single subject, during a single scanning session. Three periods of dichoptic stimulation were interleaved between four fixation-only periods in which no stimulus was present on the screen except the aperture and fixation point. The MR signal is superimposed on the reported perceptual alternations (green:motion, red:noise, yellow:piecemeal). As expected, there was a clear rise in brain activation when visual stimuli were presented, compared to the baseline

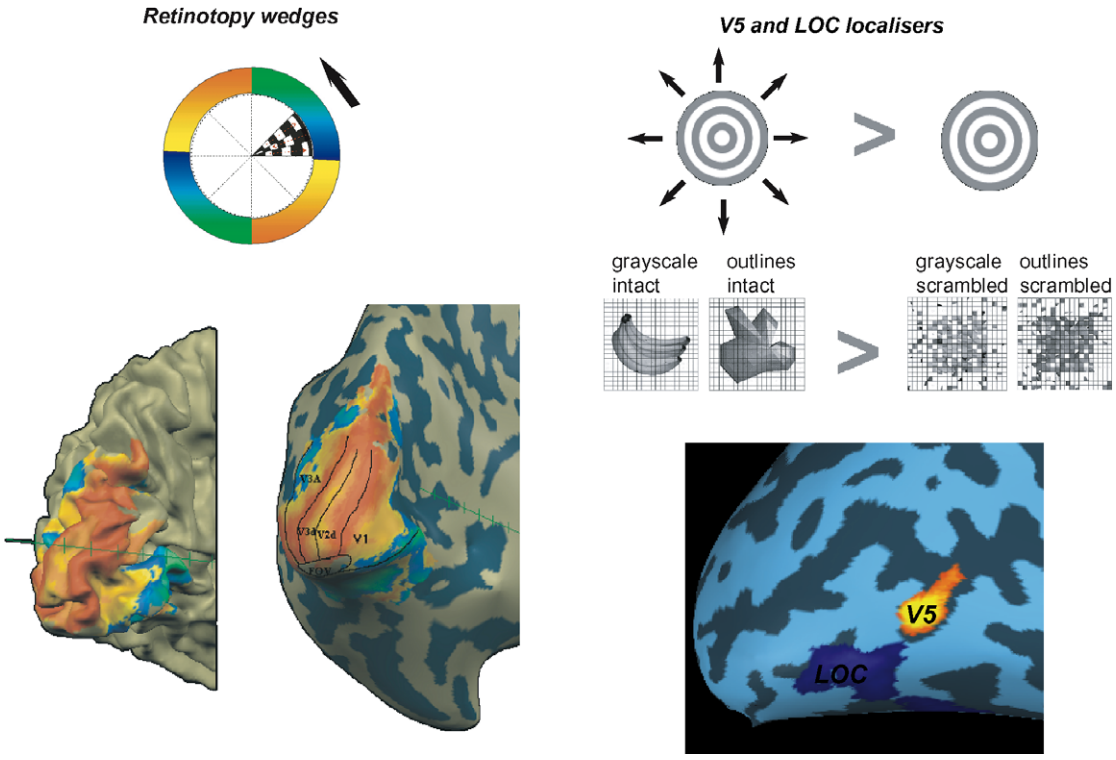

Fig. 1. Schematic presentation of the three types of localiser stimuli used in this study, together with the visual areas that they activated. Rotating, flickering luminance wedges were used to reveal the retinotopic organization of each subject's cortex. The colour coding shows the correspondence between the location of the rotating wedge in the visual field, and the part of visual cortex that was activated. Vertical and horizontal meridians were used to demarcate borders between different areas. Area V5 was accurately identified in each subject by comparing the activity evoked by expanding/contracting low-contrast luminance rings to the activity evoked by the same rings when constant. Area LOC was accurately identified in each subject by comparing the activity evoked by the presentation of intact objects to that evoked by the presentation of scrambled versions of these objects that share the same low-level properties with the original ones.

periods of fixation-only (grey). In addition, there is a further tendency of signal modulation during dichoptic stimulation: overall, activity seems to be higher when coherent motion (green) rather than random noise (red) was perceived. In order to investigate this perceptual modulation more clearly, we did event-related averaging based on the reported (or physical, in the case of the grey fixation-only condition) onsets of each event for all scanning sessions of this subject. The result is shown in Fig. 2c: Firstly, there is a reduction in brain activity at the onset ($t = 0$) of the fixation-only condition (i.e. removal of the visual stimulus), and this reduction ($\sim$0.8%) thus represents the overall MR signal modulation resulting from the random dot stimulation. On top of that, a weaker ($\sim$0.2%) but also significant modulation exists between the green (motion perception) and the red (noise perception) curves, which starts developing after the onset of the subject's response and is abolished at $\sim$7 s later. Stimulus-induced signal modulation with respect to fixation-only baseline was variable, depending on both the subject and the visual area involved. More interestingly, the effect of the perceptual state in the modulation of the MR signal was different across different visual areas within each subject.

A two way analysis of variance of all our data showed a significant condition-by-area interaction ($p < 0.01$) indicating a differential effect of perceptual alternations across the brain. Fig. 3 shows the result of averaging the event-related time courses across all subjects, separately for each of the seven different visual areas. In order to get a quantitative idea of how different the motion and noise responses were in each area, we used a Wilcoxon ranksum test (see Section 2). No statistically significant difference between coherent motion (green) and noise (red) perception was found in areas V2 and V4. Modulation in area V1 is marginally significant, the z-score of this area being almost half that of area V3, the area with the next larger z-score. The largest z-score is obtained for area V5, followed by areas V3A and LOC, all three areas having z-scores twice as big as that of area V3. Furthermore, the amplitude of the modulation in these three areas is over twice the one observed in V3, which is in turn twice as big as the one observed in V1. There is, therefore, a variability in the size and significance of the MR signal modulation resulting from perceptual motion/noise alternations across the different visual areas. In this population analysis, area V5 shows the most robust modulation, followed by areas V3A and

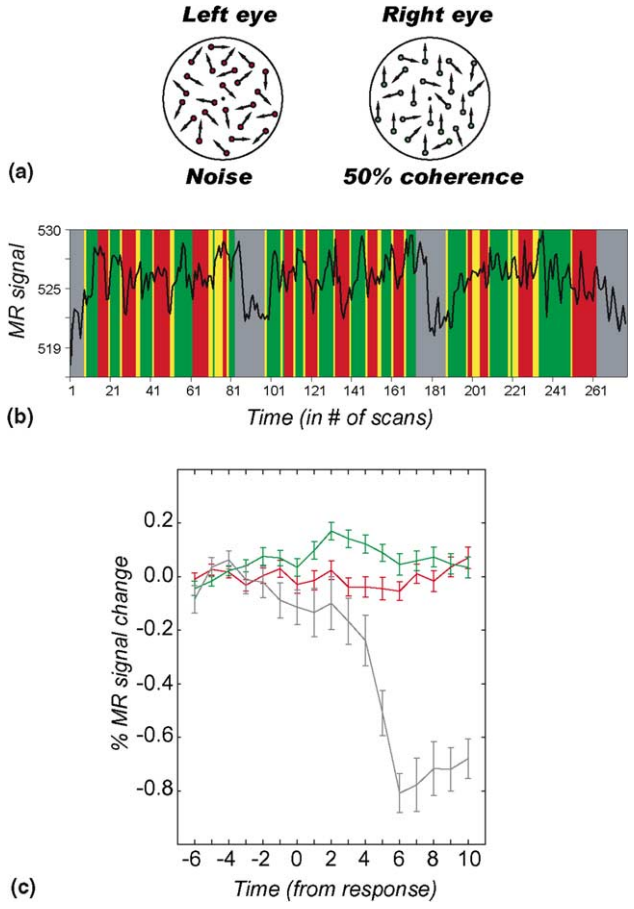

Fig. 2. (a) Schematic presentation of the BR stimuli used in this study. In the example shown here, green random dots having a 50% coherent upward motion signal are presented to one eye and red random dots at 0% coherence are presented to the other eye. In this way, binocular rivalry develops between the images in the two eyes, leading to alternating perception of red or green dots, or a mixture of the two (piecemeal rivalry). During these experiments, both the colour (red or green) of the coherently moving dots as well as the eye in which they were presented were varied. (b) Raw MR signal in area V5 of a single subject, during a single scanning session. The session consisted of three 75-s periods of dichoptic stimulation (either green, red or yellow), interleaved between four 15-s periods of fixation with no stimulus present (gray). Green indicates time periods during which the subject perceived the coherently moving dots, red indicates time periods where perception of the noise took place, and yellow indicates periods of piecemeal rivalry. Acquisition time for each volume was 1 s long. (c) Event related averaging results in area V5 of the same subject. Error bars indicate the standard error of the mean response when averaging between all similar events in a total of six scanning sessions including the one shown in b. For averaging, all responses were aligned at time 0, the time in which the subject reported a perceptual change (or visual stimulation was physically turned off, in the case of the gray). Brain activation is expressed as % MR signal change with respect to the baseline activation. The green line shows the response to motion, the red line the response to noise, and the gray line the response to stimulus removal (fixation-only condition). The latter can be used as an indication of the magnitude of activation our visual stimuli could elicit (in this particular case just under 1%).

LOC. In all these three areas, the difference between the green (motion) and the red (noise) curves starts developing a few seconds before the subject's report ($t = 0$), and stays there for until 6–7 s after. The two responses begin differentiating before the report of the subject because coherently moving dots start being perceived during piecemeal rivalry, i.e. before the establishment and report of a stable percept.

For a more detailed presentation of the data, individual results for each of the six subjects in each of the seven visual areas tested are shown in Table 1. Although there is some variability across subjects regarding the strength of the effect with respect to a certain visual area, there is consistency within each subject when comparing across areas. Areas V5, V3A and LOC are the ones with the strongest effect in all subjects, and, with the exception of V3A of subject 6, all have significantly different responses between motion and noise perception. Results are not so clear for area V3, where the difference is statistically significant for only 2/6 subjects. No statistically significant difference is found in area V2 for any of the subjects. This is also true for areas V1 and V4, with the exception of subject 1 which shows a significant effect for both these areas (but a much stronger effect for V5 and V3A, and, compared to V4, LOC as well). To summarise, the strongest and most consistent effect across subjects was found in areas V5, V3A and LOC, a not so consistent effect in area V3, and a minimal effect in areas V1, V4, and V2.

A further difference between the areas showing a differential activation due to perceptual modulation and the ones that do not, is the fact that the former do not respond to the establishment of a noise percept, whereas the latter do: Areas V1, V2, V4 and, to a lesser extent V3, increase their activity in response to the establishment of a stable percept (end of piecemeal rivalry), irrespective of what this percept is. This could reflect a top-down control mechanism, signaling the end of the competition for dominance and being controlled by 'higher' areas (Lumer, Friston, & Rees, 1998). Another possibility is that this behavior reflects some sort of 'perceptual adaptation' rebound-effect, either to colour or to motion: The non-selective response of these areas 'adapts' to the dominant perception, and is then re-excited when a new percept is established. With the exception of V3A, V5 and LOC, all other areas show a significant difference between the peaks and troughs of their response at 0%. A similar, transient increase in activity during BR perceptual alternations which is irrespective of the sign of the latter has been also reported in V1 (Polonsky et al., 2000).

Fig. 4 shows the results of a control experiment in which physical alternation was used instead of BR. Modulation amplitude in areas V3A, V5 and LOC was 1.5–2 times as big as that observed under BR. Areas V1, V2, V3 and V4 did not show a statistically significantly different activation between 50% and 0% ($p > 0.001$), further suggesting that the stimuli used here

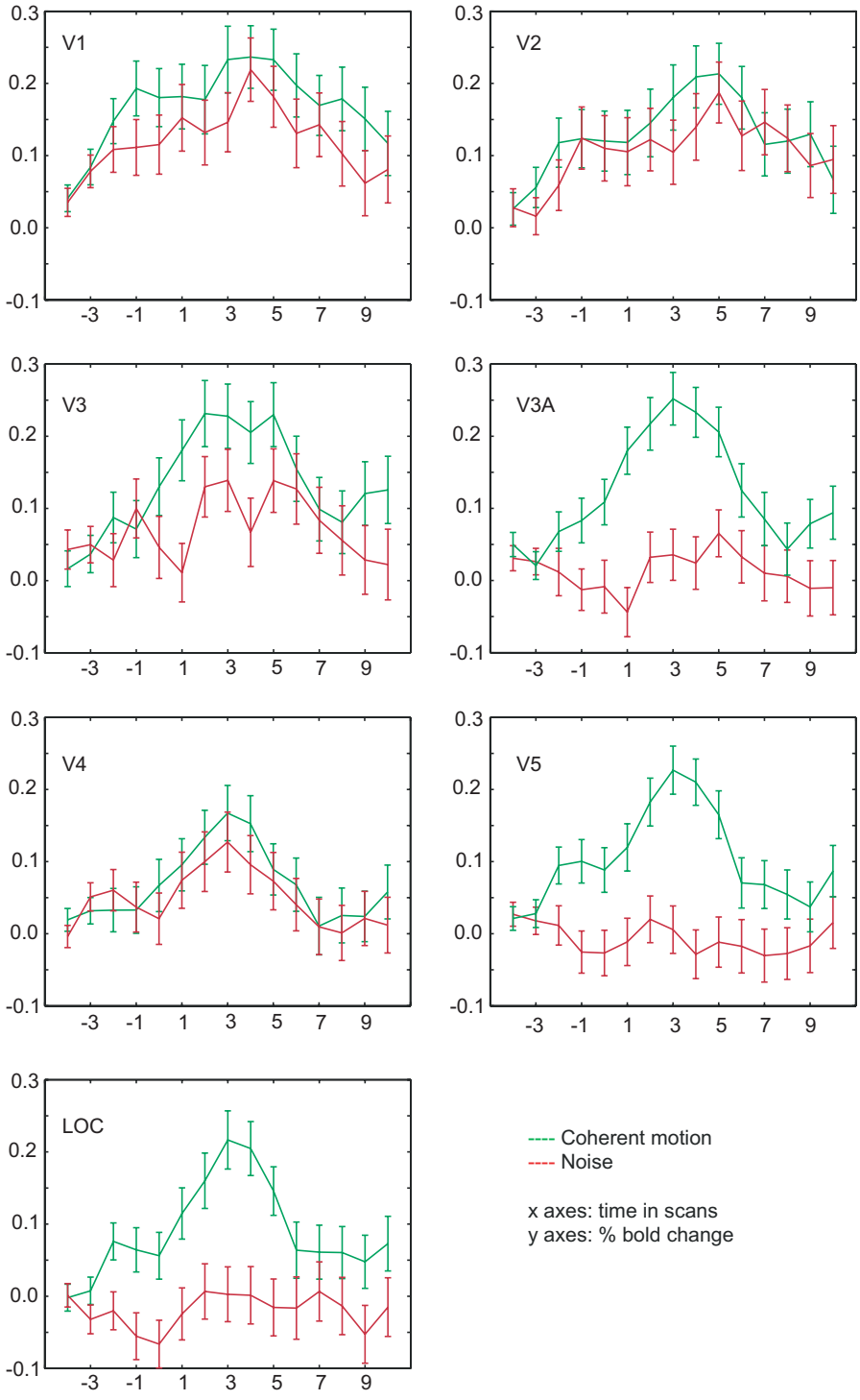

Fig. 3. Event related percent BOLD change averaged among all six subjects, for seven different visual areas. Green indicates activation when perceiving the coherent motion stimulus and red when perceiving the noise (0% coherence) stimulus. Error bars represent standard error of the mean across all events in all scanning sessions of all subjects. Wilcoxon p-values and z-scores (using a normal approximation) have been calculated for each area: V1: $p = 0.0068$, $z = 2.70$ V2: $p = 0.5111$, $z = 0.6571$; V3: $p = 3.13 \times 10^{-6}$, $z = 4.66$; V3A: $p = 3.95 \times 10^{-20}$, $z = 9.19$; V4: $p = 0.0201$, $z = 2.32$; V5: $p = 2.04 \times 10^{-25}$, $z = 10.42$; LOC: $p = 1.61 \times 10^{-20}$, $z = 9.29$.

might equally activate these areas, in which case (in the BR experiments) perceptual alternations are reflected in all areas but manifest a differential motion/noise response only in those which are selective for one stimulus versus the other. In this sense, our BR results are accurately reflecting activation properties of physical,

Table 1
A quantitative representation of the relative differences in the modulation of brain activation by motion perception, between seven different visual areas for all six subjects expressed as a *p*-value of the Wilcoxon rank-sum test

	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5	Subject 6
V1	*3.65E−05*	0.0502	0.2060	0.2767	0.0379	0.2866
V2	0.1330	0.9403	0.0473	0.4417	0.2013	0.1971
V3	*9.65E−04*	*5.54E−08*	0.0805	0.9589	0.2601	0.1712
V3A	*4.40E−08*	*1.66E−10*	0.0037	*1.32E−04*	*3.02E−05*	0.0939
V4	0.0012	0.0249	0.7025	0.9489	0.5463	0.7105
V5	*4.64E−10*	*5.82E−12*	*2.20E−05*	*2.55E−05*	*4.54E−04*	0.0055
LOC	*2.95E−04*	*2.00E−06*	0.0092	*3.14E−04*	*4.08E−06*	*2.77E−05*

Inverted values are expressed as negative powers of 10 (in matlab format).

non-rivalrous stimulation, suggesting that there is no clear distinction between the areas which are involved in motion processing and those with activity reflecting the motion percept.

To rule out the possibility that the stronger activation observed with the perception of motion was due to subjects breaking fixation and tracking the coherently moving dots, we also measured eye movements. We did not find any significant differences between the mean number, amplitude or direction of saccades when comparing periods of coherent motion perception to periods of perceiving motion noise. We did, however, find a small but consistent difference in the distribution of vertical eye position during the two conditions. Fig. 5 shows result of the subject having the more pronounced effect. In all cases, fixation was good, mostly within a 0.5° window, and never outside 1°. Nevertheless, there is a slight tendency for more eye-position data to accumulate to the left tail (upper visual field) of the distribution when perceiving upward motion, and to the right tail (lower visual field) when perceiving downward motion. This is more clearly demonstrated in the plots to the right part of the figure, showing the deviation of the distributions from a normal one. The deviation is symmetrical in the case of 'noise' perception, but biased in a consistent way in the other two cases. Also, in the former case, there is no difference between the vertical and horizontal (not shown here) eye position distributions, suggesting that our eye-tracker was equally sensitive in both directions.

4. Discussion

In the present study we used BR and fMRI in order to investigate the relationship between motion perception and the activation of human visual cortex. The most significant MR signal increase when perceiving coherent motion as opposed to random noise was found in area V5. This is an area highly specialized for motion processing, in both the monkey (Zeki, 1974) and the human (Dupont et al., 1994; Tootell et al., 1995; Zeki et al., 1991). Studies in the macaque have shown that motion perception is impaired after lesioning this area (Newsome & Pare, 1988), that the animal's psychophysical performance in direction discrimination is accurately reflected in the activity of V5 single units (Newsome et al., 1989), and can be even biased by microstimulation of this particular area of the monkey brain (Salzman et al., 1990). Furthermore, a direct link between motion perception and V5 activation has been suggested by electrophysiological monkey studies (see Section 1). In one of these (Logothetis & Schall, 1989), BR was used to demonstrate the existence of neurons changing their firing rate as a result of changes in motion perception. In agreement with this study, our present results are also consistent with a modulatory influence of perception on the activity of V5, but do not verify the existence of a subpopulation of neurons responding more to the suppression of their preferred stimulus, as reported in the monkey study. The work presented here measures the BOLD response of humans reporting under BR, instead of counting spikes in the brain of a monkey 'reporting' his percept of a single, brief dichoptic flash. Furthermore, we used motion versus a neutral stimulus, rather than two motion stimuli of opposite directions. A direct comparison of the two studies is therefore not suitable beyond the point that both show a perceptual modulation effect in this area. The present study is closer to other human fMRI studies, relating motion perception to V5: this area is activated by illusory motion from a stationary stimulus (Zeki, Watson, & Frackowiak, 1993), when the same counter-flickering stimuli appear as moving rather than as blinking (Muckli et al., 2002a), and modulates its firing with perceptual switches between pattern/component motion perception (Castelo-Branco et al., 2002; Muckli, Singer, Zanella, & Goebel, 2002b). In addition, the study of a patient with a total loss of area V1 showed that he might or might not perceive a motion stimulus, depending on the magnitude of V5 activation (Ffytche, Guy, & Zeki, 1996). Our results verify the importance of V5 in motion perception and go further to show that, among all visual areas, it has the strongest correlation with motion perception in the brain.

In addition to V5, two other areas clearly show a strong increase in activity accompanying motion perception: V3A and LOC. The involvement of the former area

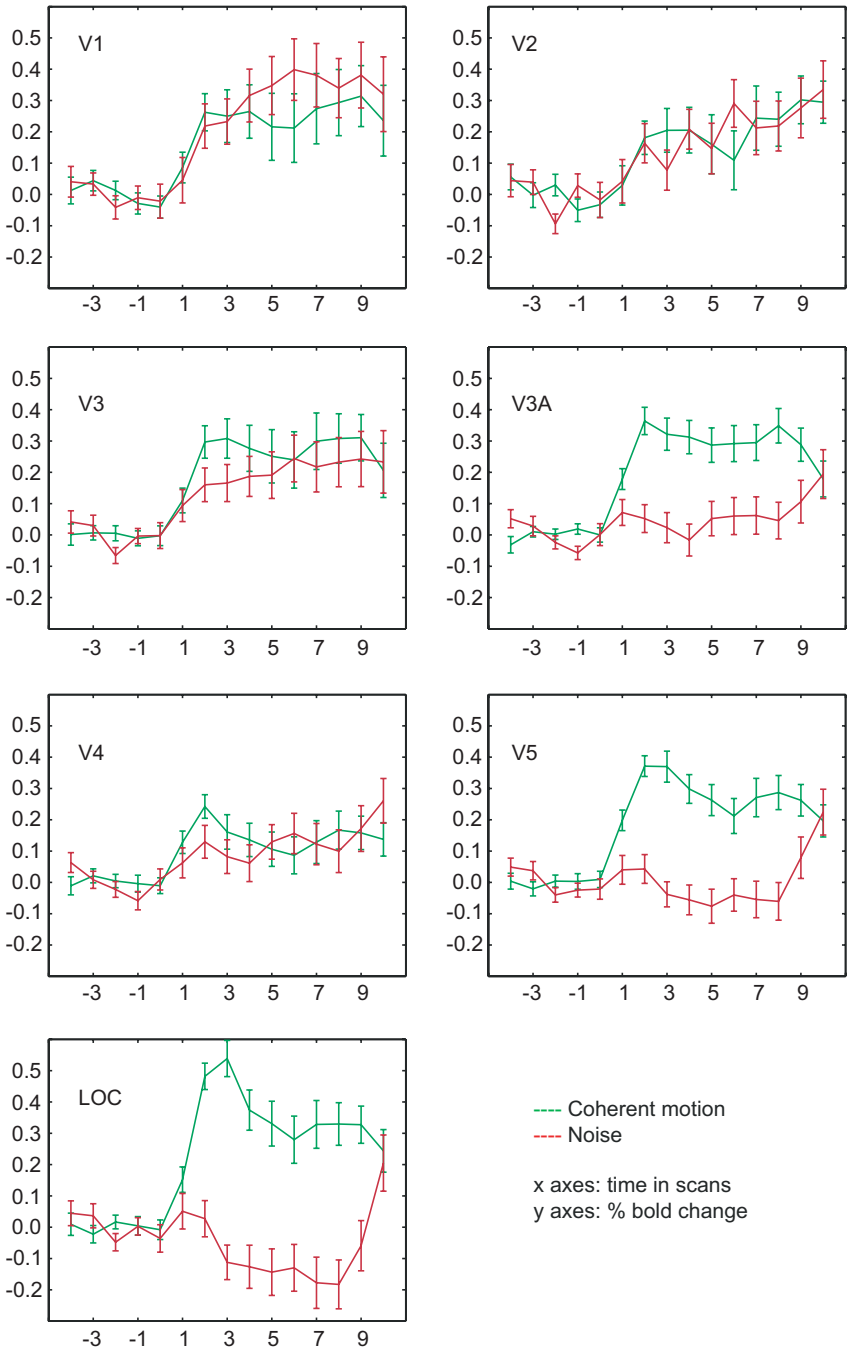

Fig. 4. Like Fig. 3 but for physical alternations. Only areas V3A, V5 and LOC show a statistically significant difference ($p < 0.001$) between coherent-motion and motion-noise activations.

to motion processing is well established: In the human, this area is equally activated by motion as is area V5 (Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998), including random dot motion (Braddick et al., 2001), and shows speed-dependent responses similar to V5 (Chawla et al., 1999). In the monkey, directionally selective neurons are present in area V3A, although to a lesser extend than in area V3 (Gaska, Jacobson, & Pollen, 1988). In this sense, our results might seem slightly unexpected, since we found a stronger effect in area V3A than in area V3. However, fMRI studies directly comparing human and monkey motion activation, suggest that area V3A is much more, and area V3 much less motion sensitive in humans than in their simian counterparts (Orban et al., 2003; Tootell et al., 1997) and that, in general, V3A in the human has properties more similar to monkey V3 (Singh, Smith, & Greenlee, 2000). Human fMRI results show that V3A is, together with V5,

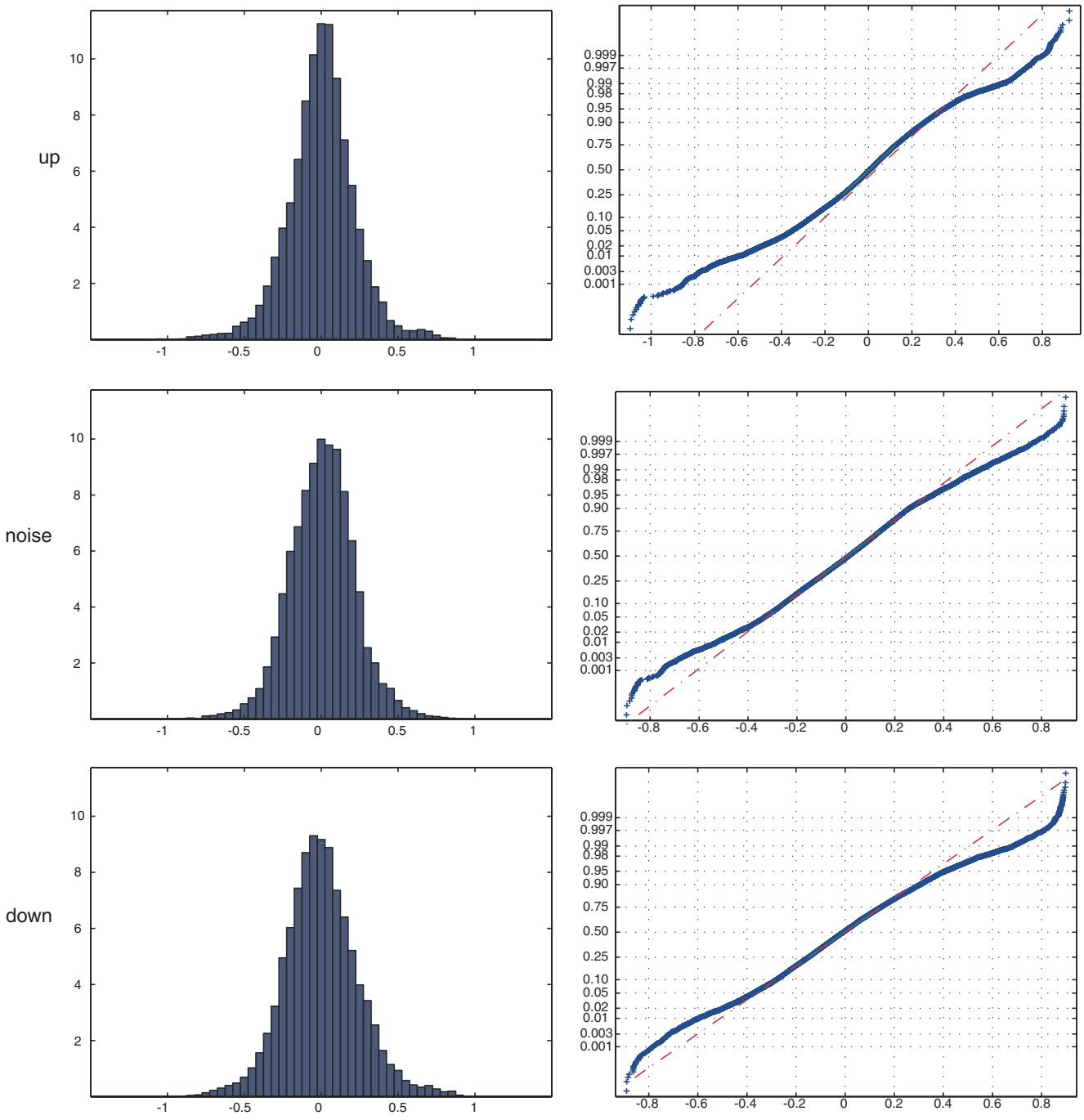

Fig. 5. The distribution of vertical eye positions of a single subject during the perception of coherent motion (up, down) and motion noise. Histograms of the distribution with respect to the center point (at 0, positive is lower visual field, negative is upper visual field) are plotted on the left (*x*-axis: vertical displacement in degrees, *y*-axis: percentage of the total population). To the right, normal probability plots are used to compare the distribution of each data set (blue) to a normal distribution (red line) connecting the 25‰ and 75‰ of the original distribution. Upward motion: mean = 0.0024, median = 0.0068, std = 0.2189. Downward motion: mean = 0.0021, median = −0.0077, std = 0.2417. Noise: mean = 0.0079, median = 0.0117, std = 0.2124.

activated by imagery motion experiments (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998), suggesting further a role for this area in motion perception that is dissociated from any sensory representation.

The LOC result, on the other hand, is somehow surprising. Not only there are is no established link between LOC activity and motion perception, but even the involvement of this area to motion processing is still unclear. LOC is considered to be an object-sensitive area, representing higher-level shape information rather than simple image features (Grill-Spector, Kourtzi, & Kanwisher, 2001). An indirect relationship between

LOC activity and motion stimulation has been previously demonstrated, as this area also responds to moving objects (Yin, Shimojo, Moore, & Engel, 2002) and shapes defined by motion (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998). The primary factor affecting LOC responses, however, seems to be the shape rather than the motion: shape-from-motion experiments have shown LOC to persist responding after the motion has stopped but the object percept is still persisting (Ferber, Humphrey, & Vilis, 2003). In short, there is a connection between motion information and area LOC, but perhaps so that this information can be used to extract different objects in the visual field. Concerning motion alone, previous studies have found area LOC to be activated, together with V3A and V5, by pure random-dot coherent motion, similar to the one used in the present experiment (Murray, Olshausen, & Woods, 2003). Our results are the first to show that activity in area LOC strongly correlates with the motion percept reported by subjects. They suggest an involvement of this area in the elaboration of the motion percept by the brain.

Negative results are usually not important in fMRI studies, as no firm conclusions can be drawn by them. In our experiment, we did not find any differential activation between motion and noise in areas V1, V2 and V4. This is probably an expected result for V4, as this area has little to do with motion (Zeki, 1973) but is instead more involved in colour processing, in both monkey (Wade, Brewer, Augath, Logothetis, & Wandell, 2003; Zeki, 1973) and human (Lueck et al., 1989; Zeki et al., 1991). It is therefore not surprising that this area does not respond more to the perception of motion than to the perception of noise during rivalry, as it does not do so during normal stimulation either. A similar explanation can probably account for the absence of any effect in areas V1 and V2 as well. Unlike V4, both these areas are important stages of the motion processing system, with direction selectivity being firstly established in layers 4B and 6 of V1 (Gouras, 1974; Hawken et al., 1988; Hubel & Livingstone, 1990), and clearly present in area V2 as well, especially in 'thin' cytochrome oxidase stripe regions (DeYoe & Van Essen, 1985; Livingstone & Hubel, 1987; Shipp & Zeki, 1985; Shipp & Zeki, 1989). However, in a control experiment where we used physical alternations instead of binocular rivalry, we were unable to demonstrate a differential activation between 50% and 0% in either of these areas. Previous studies have contradicting results with respect to V2, one group reporting a linear increase in activation with motion coherence (Rees, Friston, & Koch, 2000) and another not finding any difference (Braddick et al., 2001), but both agree in the absence of an effect of% coherence changes in striate cortex. Given that fMRI activity in these early areas has been shown to modulate by perceptual alternations in other low-level properties such as contrast and orientation (Polonsky et al., 2000; Tong & Engel, 2001), together with their involvement in motion processing, it is quite likely that they can also be modulated by changes in motion perception. Further experiments, using more appropriate stimuli, are necessary to answer this question. In the present study, the lack of any modulation in these three areas serves as a good control that the effect we get in other areas is indeed specific to motion perception (and not to, for example, a general increase in attention—see below).

Attention has been previously shown to modulate the activity in area V5 (Rees, Frith, & Lavie, 1997). Furthermore, studies of motion related V5 activity have suggested that subjects attend more to a moving stimulus compared to a stationary one (Huk, Ress, & Heeger, 2001). However, we do not believe that the increased brain activation during perception of coherent motion that we report here is due to attention. Firstly, we did not use a moving versus stationary paradigm. The 0% coherence stimulus is not static but as dynamic as the 50% one, a fact being also reflected in the balanced BR that we observed between the two. Secondly, subjects had to attend to the colour (not the motion) of the stimuli, equally throughout the session and irrespective of the motion percept, in order to accurately report their alternating perception. Finally, given that attention can modulate activity throughout the visual brain (see Watanabe et al., 1998 for V1 motion, or Kanwisher & Wojciulik, 2000 for a review), if the effect we got here was due to a general increase in arousal during the perception of coherent motion, it should have manifested itself in all of the areas that we examined.

Any perception-specific eye movements are also not able to account for the results reported here. The small eye position distribution bias that we found (see Results) is of negligible magnitude compared to that of the eye-movement effects previously reported to elicit a differential response (Freitag, Greenlee, Lacina, Scheffler, & Radu, 1998). In addition, V5 neurons responding to eye movements in the monkey have been shown to prefer pursuit of small single light spots rather than larger patterns of random dots (Komatsu & Wurtz, 1988), and V5 responses are actually related to target image motion on the retina rather than to the eye movement per se, both in monkeys (Ilg & Their, 2003; Newsome, Wurtz, & Komatsu, 1988) and in humans (Dukelow et al., 2001). Furthermore, eye movements have been found to also increase the activity in areas such as V1 (Martinez-Conde, Macknik, & Hubel, 2000) and V2/V4 (Leopold & Logothetis, 1998). Therefore, even if selective eye movements during motion perception influenced MR signal in our study, they cannot account for the specificity and magnitude of the modulation effect we report here.

To conclude, in several of the areas under study, the brain activation was greater during periods in which coherent motion was perceived compared to periods during which motion noise was perceived. Our results

clearly support a V5 involvement in the perception of coherent motion, but in addition show that this is not the sole area reflecting motion perception, and that other visual areas as well correlate their activity in accordance to motion perception, almost as strongly as V5. Therefore, although V5 has the strongest correlation than all other areas, it is inappropriate to attribute the perception of visual motion to a single area alone—it rather seems that motion perception arises as a result of synergy between a number of different areas involved in the processing of this attribute.

Acknowledgements

We would like to thank colleaques at the MPI for helpful comments on the manuscript. This work was supported by the Max Planck Society, Deutsche Forschungsgemeinschaft grant (DFG, TH 812/1-1) and EMBO (Long Term Fellowship ALTF-2001 awarded to K. Moutoussis).

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